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AGE AND SEX DIFFERENCES IN WING LOADING AND OTHER AERODYNAMIC CHARACTERISTICS OF SHARP-SHINNED HAWKS

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Wing area, wing loading and other aerodynamic characteristics are particularly important for the diurnal raptors, birds that spend considerable time on the wing or rely on agility in flight for the capture of prey. Brown and Amadon (1968) summarize data available on wing loading for various Falconiformes and list measurements for only 56 species. Of these 56, exactly half of the wing loadings are based on a sample of only one, both sexes were measured for only seven species and age was not noted for any. In this paper we examine age and sex differences in wing area, wing loading and other aerodynamic characteristics of Sharp-shinned Hawks (*Accipiter striatus*) based on a sample of 255 wings and 108 tails. The hawks were captured in a variety of traps (see Bub 1974) at the Cedar Grove Ornithological Station, on the western shore of Lake Michigan near Cedar Grove, Sheboygan Co., Wisconsin. A description of the Cedar Grove region can be found in Mueller and Berger (1966) and an account of the migrations of sharp-shins is given in Mueller and Berger (1967).

TECHNIQUES

Birds were measured on the day they were captured. Wing chord was measured by placing the wrist (bend) of the wing at the zero point of a rule and pivoting the folded wing downward until the tip of the longest primary just touched the rule. Tail length was measured by inserting a thin metal rule between the central rectrices and sighting across the tops of the longest rectrices of the folded tail. Both linear measurements were taken to the nearest mm. Birds were weighed to the nearest gram on a balance graduated in 0.1 g increments. Esophageal ("crop") contents, if any, were estimated and subtracted from the gross weight.

The right wing of a hawk was photographed while the ventral side was held against a vertical, rigid sheet of clear plastic ruled into 5 cm squares (Fig. 1). In addition to the squares a 10 × 30 cm rectangle was outlined in fine black tape. A white window shade about 1 m behind the plastic provided contrast. The body of the hawk was held with one hand against the edge of the plastic and the wing was held by the manus with the other hand so that the wing was barely in contact with the plastic. Another person photographed the wing, stationing himself normal to the wing. The date, age, sex and band number of the hawk were affixed to the plastic and included in the photograph.

The negatives of the wing photographs were mounted in slide holders and projected to life size using a projector with a zoom lens and matching the 10 × 30 cm rectangle with one drawn on the screen. The outline of the wing was traced on a piece of paper, along with an estimated half width of the body. In some photographs the wing was pulled away from the body, exposing the axillars. The axillars were not included in the measurement of wing area. The tracing was measured to the nearest 0.1 cm^2 with a compensating polar planimeter.

FIG. 1. Photograph of spread of wing of a Sharp-shinned Hawk.

Each tracing was measured twice, or until 2 measurements were obtained that differed by less than 1%. In a test of the accuracy of wing measurement the wing of 1 hawk was photographed 15 times. Holders and photographers were alternated quasi-randomly among the three authors. Each of us held the bird 5 times. Between photographs, the bird was returned to its holding tube for at least a few minutes. An analysis of variance revealed no significant difference among holders. The area for the right wing was 272.43 ± 10.18 (SD), yielding a standard error of measurement of 2.07% at the 95% confidence interval.

On the tracing, wing length was measured from the tip of the longest primary to the body. Wing span was obtained by adding wing length to the measurement of half body width and multiplying by 2. Average wing width was calculated by dividing the area of one wing by wing length. Aspect ratio was obtained by dividing wing length by wing width. The wing area given in Table 1 was obtained by multiplying the area of the measured wing by 2. Wing load was calculated by dividing the weight of the bird by its total wing area.

Holding the tail of a live bird for photographing the area is difficult. Tails were held up against the vertical plastic used for wing measurements (Fig. 2). Angles of spread varied from 41°–111°. Photographic negatives were projected and traced using the same methods as for wings. The base of the tail was obscured by the holder, and we resorted to the following adjustments. A straight edge was oriented along the outer edge of the outermost rectrix on the tracing and a line drawn extending the base of the tail (dashed lines in Fig. 3). This procedure was repeated for the other side of the tail so that the two extended lines met. The angle thus formed (A) was measured as the angle of spread. The distance from the apex of

TABLE 1
WING AREA AND RELATED MEASUREMENTS FOR SHARP-SHINNED HAWKS

Measurements	Adult ♂♂ N = 54 $\bar{x}$ ± SD	Juvenile ♂♂ N = 90 $\bar{x}$ ± SD	Adult ♀♀ N = 54 $\bar{x}$ ± SD	Juvenile ♀♀ N = 57 $\bar{x}$ ± SD
Wing chord (cm)	17.24 ± 0.33**[a]	16.88 ± 0.32	20.22 ± 0.78**	19.92 ± 0.35
(corrected)	(17.15)**	(16.87)		
Wing length (cm)	24.35 ± 0.72**	23.77 ± 1.02	28.52 ± 1.10**	27.75 ± 0.73
Wing width (cm)	8.91 ± 0.31*	8.83 ± 0.24	10.33 ± 0.44*	10.20 ± 0.30
Wing span (cm)	53.06 ± 1.45**	51.98 ± 2.06	64.02 ± 2.18*	62.21 ± 1.47
Aspect ratio	2.74 ± 0.12**	2.69 ± 0.11	2.76 ± 0.13*	2.72 ± 0.09
Wing area (cm^2)	434.06 ± 20.78**	419.93 ± 25.78	589.77 ± 38.85**	565.29 ± 24.84
(corrected)	(429.94)*	(420.63)		
Weight (g)	101.24 ± 6.42**	96.43 ± 5.97	176.26 ± 11.57**	163.38 ± 9.03
(corrected)	(102.89)**	(97.50)		
Wing load (g/cm^2)	0.233 ± 0.02	0.230 ± 0.02	0.300 ± 0.03**	0.289 ± 0.02
(corrected)	(0.239)**	(0.232)		

* Differs significantly from juveniles, $P < 0.05$, t-test, 1-tailed; ** differs significantly from the juveniles, $P < 0.01$.
[a] Significantly larger than the mean given in Mueller et al. (1979), $P < 0.05$, t-test, 2-tailed. Corrected means for wing chord and weight are from the larger sample of Mueller et al., (1979). Corrected wing areas are based on regressions of area on wing chord.

this angle to the longest rectrices was measured (B), and from this measurement we subtracted tail length (D, as measured from the live bird). This difference (C) was then measured from the apex of the angle and an arc drawn across the tail with a compass (dashed line). The tail area measured with the planimeter included everything within solid and dashed lines except the basal segment of the circle with radius C (Fig. 3). Since tail area varies with angle of spread, we developed a formula which estimates tail area. We first calculated for each tail: (sin A)(length^2), where A is the angle of spread and length is the tail length measured from the live bird. We then calculated a linear regression for all 108 tails, giving us the formula:

$$\text{Area} = 4.1189 + 0.9624(\sin A[\text{length}^2]).$$

The equation is an excellent fit to the data ($r = 0.98$).

RESULTS

Wing photographs were taken when sufficient personnel were available, and the sample of 255 wing area photographs was not randomly distributed throughout the autumn. We have found that the population of Sharp-shinned Hawks caught at Cedar Grove shows complex changes in wing chord and weight through the autumn (Allez et al., unpubl.), and the birds sampled for wing areas thus might not be representative. We compared wing chord and weight from our sample for wing areas with wing chord and weight from a sample of almost 2000 birds taken from the entire season in the years 1953–1964 (Mueller et al. 1979).

FIG. 2. Photograph of spread of tail of a Sharp-shinned Hawk.

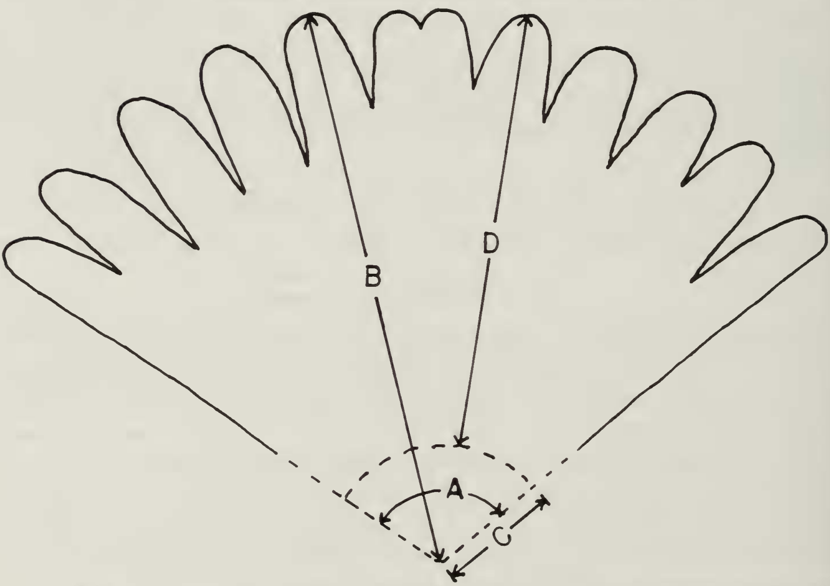

FIG. 3. Method of measuring tail area. The solid lines are traced from Fig. 2. See text for explanation of dashed lines and symbols.

Only one measurement from the sample wing areas differed significantly (t-test, $P < 0.05$, 2-tailed) from those of the larger sample—adult males had significantly longer wing chords in the sample taken for wing area. In addition, these adult males were almost significantly lighter in weight ($P < 0.08$). Since wing area is in part a function of wing length, our sample of wing areas for adult males thus overestimates wing area and underestimates wing loading. To obtain better estimates, we performed linear regressions of wing chord on wing area for both adult and juvenile males and then calculated "corrected" wing areas and wing loadings based on the mean wing chords and weights from the larger sample of Mueller et al. (1979).

Adults of both sexes are significantly larger than juveniles in all measurements: wing chord, wing length, wing width, wing span, aspect ratio, wing area, weight and wing loading; with one exception—the wing loading of males (Table 1). However, the corrected estimates of wing loading of males, based on the larger, more representative sample, show a significantly greater wing loading for adults than juveniles, as well as significantly greater wing chord, wing area and weight. Two differences between adults and juveniles are disproportionate: (1) the increase in width of wings in adults is less than half the increase in wing length, resulting in a higher aspect ratio in adults, and (2) the increase in wing area in adults is proportionately only about half as great as the increase in weight resulting in higher wing loading in adults. Females of both age groups are significantly larger than males ($P < 0.0001$) in wing chord, wing length, wing width, wing span, wing area, weight and wing loading but do not differ significantly in aspect ratio ($P > 0.05$, Table 1).

Estimated tail areas for three angles of spread are presented in Table 2. The tail lengths used to calculate areas using the regression equation are the means from Mueller et al. (1979) because three of the four means from the samples taken from tail photographs differed significantly from the means from the larger sample. We have examined spread tails in many live Sharp-shinned Hawks, a few dead individuals and the 102 photographs for tracings; in all of these, of course, the tail was spread manually by us. We estimate that a Sharp-shinned Hawk in normal flapping flight has its tail spread about 15°. We estimate that the maximum possible spread, without separation of rectrices, is about 100°. The tail shown in Figs. 2 and 3 is spread 107°. At 120° of spread there is some separation of rectrices, and the areas presented for this angle of spread probably are overestimates. In Table 2 we also present total flight surface area (wings plus tail) and the loading of total flight surface. The tail areas of juveniles average about 3% greater than that of adults. The total flight surface area of adults is greater because adults have greater wing areas than juveniles (Table 1). Tail area constitutes only about 10% of the total flight surface

TABLE 2
ESTIMATED TAIL AREAS IN SHARP-SHINNED HAWKS

Age	Sex	Area (cm^2)	Total surface[a]	Load[b] (g/cm^2)
		Tail spread 15°		
Adult	♂	47.75	477.69	0.215
Juvenile	♂	49.17	469.80	0.208
Adult	♀	64.50	654.27	0.269
Juvenile	♀	66.03	631.32	0.259
		Tail spread 100°		
Adult	♂	201.97	631.91	0.163
Juvenile	♂	208.39	629.02	0.155
Adult	♀	277.94	867.71	0.203
Juvenile	♀	284.84	850.13	0.192
		Tail spread 120°		
Adult	♂	256.99	686.93	0.150
Juvenile	♂	265.19	685.82	0.142
Adult	♀	354.08	943.85	0.187
Juvenile	♀	362.90	928.15	0.176

[a] Wing and tail area.
[b] Total surface load.

area when the tail is spread 15°, but when the tail is spread 100° the tail constitutes about a third of the total flight surface area. The difference between adults and juveniles in total flight surface area is about 1.7% (males) to 3.6% (females) when the tail is spread 15°. This difference decreases to 0.5% and 2.1%, respectively, when the tail is spread 100°.

The total surface loading is about 3.5% greater in adults when the tail is spread 15°; this difference increases to about 5.5% when the tail is spread 100°. Juveniles thus have considerably lower flight-surface loadings when the tail is spread.

DISCUSSION

Adults are larger than juveniles in every measurement taken except tail length and tail area; adults are larger than juveniles in many animals but in birds the restrictions imposed by flight and the persistence of non-growing remiges and rectrices for a year or longer impose severe limits on the magnitude of age differences. Birds cannot gradually increase in size; the change is rapid as old flight feathers are replaced by new. A large change in the length of remiges would require compensatory large and rapid changes in musculature and perhaps even in the skeleton or in large changes in flight and foraging behavior. Mueller and Berger (1970) have shown that sharp-shins require considerable experience to perfect predatory techniques; rapid transitions in these behaviors are unlikely. The differences in size between adult and juvenile Sharp-shinned Hawks are small, but are statistically significant, and we believe that there is an adaptive rationale for these differences.

A bird is able to fly because an airfoil moving through the air generates lift. A bird moving through the air also induces drag, turbulent eddies which reduce its speed. Much of the induced drag is generated by vortices at the tip of the wing. In gliding flight, aerodynamic efficiency is maximized by increasing the aspect ratio of the wing (length/width), in effect decreasing the portion of the total wing area which is at the tip where lift is diminished by induced drag. In flapping flight a long wing is less "efficient" because it requires more power to move a long wing than a short one. A gliding bird has a minimum (stalling) speed. Flight is impossible at slower speeds because the airflow over the wings breaks up into turbulent eddies and lift is lost. Stalling speeds are a function of wing loading (the weight carried by the wing area). High wing loadings produce high stalling speeds and low wing loadings permit birds to fly more slowly. A bird can maintain flight speed by decreasing its angle of attack (the angle the wing makes with the horizontal), and thus losing altitude, or by powered flight (flapping its wings). A soaring bird is actually gliding downward but the air is rising more rapidly than the bird is sinking. A bird with a light wing loading can glide more slowly than a bird with a heavy wing loading and thus will rise more rapidly in a given updraft and and be able to use less powerful updrafts. Low wing loadings and lower stalling speeds also increase maneuverability.

Tails also contribute to lift, particularly in slow, soaring flight; this is why hawks spread their tails when soaring in an updraft. Although tails do not produce as much lift per unit area as wings, a bird with a longer tail and larger tail area when spread may have some advantage over a bird with a shorter tail and less tail area. This is because a folded tail induces little drag in flapping flight, need not be flapped as a wing, but is available for added lift when needed. The main advantage of increased tail area, however, is that it enhances maneuverability. Large "reserve" control area, as produced by a spread tail is of particular advantage at slow flight speeds since the force produced by a deflecting surface is proportional to the area of the surface and the square of air speed. Birds which fly rapidly thus need smaller control surfaces than those which fly slowly. (For a more detailed, yet comprehensible, explanation of bird flight see Barlee 1964.)

The above aerodynamic considerations lead to the conclusions presented below. The low wing loadings of juvenile sharp-shins give them the potential of using lighter updrafts than adults, a capability which is further enhanced by the large tail area. Shorter wings require less power to flap and hence less energy consumption than longer-winged adults. All of these considerations suggest that juveniles expend less energy in flying than do adults. The light total surface loadings of juveniles provide them with inherently greater maneuverability than adults, with the large tail area playing an important role.

Adults weigh more than juveniles and this difference is almost certainly not the result of fat deposition and is most likely due to larger flight muscles in adults (Mueller et al. 1979). The greater weight, larger wing muscles, greater wing loading and greater aspect ratio of adults should produce a more rapid and powerful flight and a greater force in striking prey than that of juveniles, but at the expense of greater energy expenditure. The apparent loss in aerodynamic maneuverability in adults may well be compensated for by the greater power and experience of adults as compared to juveniles. Adults are thus faster, higher performance "flying machines" than juveniles, but require higher energy expenditures and thus higher food consumption than juveniles.

Adults thus appear to be an "optimal design" for rapid and powerful pursuit of prey and the juveniles a lower performance configuration, but one which is inherently more maneuverable and requires less energy consumption and expenditure. As juveniles gain experience they can afford the adult configuration; both aerodynamic forms are thus adaptive. Readers should be reminded that the above conclusions are based on morphometric measurements and aerodynamic considerations; direct measurements of performance and metabolic needs are lacking and would be extremely difficult, if not impossible, to obtain.

SUMMARY

Adult sharp-shins have significantly longer and wider wings, greater wing areas, higher wing loadings and higher aspect ratios than juveniles. Juveniles have longer tails and greater tail areas than adults. Within an age class, females are larger than males in all of the above measures except aspect ratio. The differences in aerodynamic characteristics between the age classes permit and obligate adults to fly faster, result in greater striking force at prey, and probably require more energy consumption than in juveniles. Juveniles are more maneuverable and probably require less energy in flight. The higher weight of adults is probably due to increased flight musculature and the added power, plus experience, probably compensate for the aerodynamic disadvantages of adults as compared to juveniles.

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LITERATURE CITED

BARLEE, J. 1964. Flight. Pp. 299–307 *in* A new dictionary of birds. (A. L. Thomson, ed.). Nelson, London, England.

BROWN, L. AND D. AMADON. 1968. Eagles, hawks, and falcons of the world. McGraw-Hill, New York, New York.

BUB, H. 1974. Vogelfang und Vogelberingung. Teil III. A. Ziemsen, Wittenberg-Lutherstadt, E. Germany.

MUELLER, H. C. AND D. D. BERGER. 1966. Analyses of weight and fat variations in transient Swainson's thrushes. Bird-Banding 37:83–112.

——— AND ———. 1967. Fall migration of Sharp-shinned Hawks. Wilson Bull. 79:397–415.

——— AND ———. 1970. Prey preferences in the Sharp-shinned Hawk: the role of sex, experience and motivation. Auk 87:452–457.

———, ——— AND G. ALLEZ. 1979. Age and sex differences in size of Sharp-shinned Hawks. Bird-Banding 50:34–44.

DEPT. ZOOLOGY AND CURRICULUM IN ECOLOGY, UNIV. NORTH CAROLINA, CHAPEL HILL, NORTH CAROLINA 27514 (HCM) AND CEDAR GROVE ORNITHOLOGICAL STATION, ROUTE 1, CEDAR GROVE, WISCONSIN 53013 (DDB, GA). ACCEPTED 19 MAR. 1981.